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Assessing Extinction Risk for West Coast Salmon

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Edited by Alec D. MacCall¹ and Thomas C. Wainwright²

- Southwest Fisheries Science Center Santa Cruz Laboratory
 Shaffer Road
 Santa Cruz, California 95060
- Northwest Fisheries Science Center Fish Ecology Division
 2032 SE OSU Drive Newport, Oregon 97365

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U.S. DEPARTMENT OF COMMERCE

Donald L. Evans, Secretary

National Oceanic and Atmospheric Administration

Vice Admiral Conrad C. Lautenbacher, Jr. USN (Ret), Administrator

National Marine Fisheries Service William T. Hogarth, Assistant Administrator for Fisheries

Ecosystem Diversity and the Extinction Risk of Pacific Salmon and Trout

Thomas H. Williams

Department of Fisheries and Wildlife 104 Nash Hall Oregon State University Corvallis, Oregon 97331

Gordon H. Reeves

U.S. Forest Service Pacific Northwest Research Station 3200 SW Jefferson Way Corvallis, Oregon 97331

(The following represents our thoughts and the literature at the time of the symposium. The conservation and recovery of Pacific salmonids in the context of landscape dynamics has been fertile ground for research. In the past few years there has been much development and refinement of the underlying concepts.)

The landscape within the distributional range of Pacific salmon and trout (*Oncorhynchus* spp.) is dynamic in space and time. Geologic processes of glaciation and volcanism have shaped a large portion of the area (McPhail and Lindsey 1986). Other events such as fire and flood have shaped the landscape at smaller temporal (10¹–10² years) and spatial scales (watersheds and basins) (Benda 1994). These various disturbances created a shifting mosaic of abiotic and biotic conditions across the range of these fish (Reeves et al. 1995). Pacific salmon and trout are adapted to dynamic environments through life-history attributes that include straying by adults, relatively high fecundity rates, variability in age of ocean entry, variability in age structure, and mobility of juveniles (Reeves et al. 1995).

Human development of western North America has modified this mosaic of conditions and has modified the temporal and spatial distribution of the habitat conditions that Pacific salmon and trout encounter. Declines of Pacific salmon and trout populations (Nehlsen et al. 1991) and other fish species in the Pacific Northwest (Williams et al. 1989, Frissell 1993) have been observed, in part, as a result of these changes. Variability in abiotic and biotic conditions has been modified and constrained to such an extent that opportunities for Pacific salmon and trout to persist have been reduced (Reeves et al. 1995). This reduction and simplification of system diversity has occurred over various temporal and spatial scales.

Ecosystem diversity, for our purposes, represents the variability of states or conditions in the freshwater ecosystem. An ecosystem is a series of states or conditions, each with given physical and associated biological features. The particular state present at a location is primarily a function of the time since the last major disturbance and the geomorphic setting. The state or

condition of a location can be thought of as a function of the disturbance history and recovery rate, with the recovery rate highly dependent on the geomorphic setting (e.g., alluvial stream reach vs. a high-gradient stream reach). Within a basin or across a number of basins, there may be a mosaic of conditions that are dynamic in space and time.

The spatial and temporal shifting mosaic character of freshwater ecosystems is a critical component in our definition of ecological diversity. Ecosystems are a result of diverse and complex abiotic and biotic interactions occurring over several decades to centuries at the river basin scale. Understanding systems at these temporal and spatial scales is difficult because past processes and interactions are often matters of surmise. But an understanding, or recognition, of these processes is needed because it may be this diversity of conditions that provides opportunities for the development of life-history variability and for persistence of salmon and trout populations. Lack of ecosystem diversity could result in lower phenotypic diversity among individuals and a scarcity of available habitat across the landscape (den Boer 1968, Poff and Ward 1990). Appropriate scales of time and space for ecosystem conditions to move through various stages need to be considered if ecological diversity is to be protected or restored (Reeves et al. 1995). In this context, consideration of ecological diversity invites questions concerning the role of dynamic environments in shaping the structure of populations and how one might incorporate this diversity in analyses of the extinction risks of Pacific salmon and trout.

The Pacific Northwest region is a highly dynamic environment over shorter, temporal (less than 300 years) scales. Understanding the structure of local species assemblages requires a reference to regional-scale phenomena (Gaston 1996). For example, the natural disturbance regime in the central Oregon Coast Range includes infrequent stand-resetting wildfires and frequent flood events that may result in concentrated landsliding into stream channels and debris flows (Reeves et al. 1995). These naturally occurring disturbances have immediate (e.g., direct mortality, habitat loss, barriers to migration) and long-term implications (e.g., introduction of essential habitat elements – large wood and sediment, alteration of channel morphology) for Pacific salmon and trout. This episodic delivery of materials causes stream channels to alternate between aggraded and degraded sediment states, and therefore, a natural mosaic of habitat conditions (i.e., range of channel conditions) exists within and among watersheds (Reeves et al. 1995). In the central Oregon Coast Range, conditions ranged from channels aggraded with sediment and little large wood, to a variety of substrates and intermediate amounts of large wood, to bedrock and large quantities of large wood. All conditions were historically found on the landscape (Benda 1994); however, they were not necessarily in equal proportions. A given watershed potentially experienced the range of these conditions over time.

Reeves et al. (1995) found that each ecosystem condition they encountered had an associated fish assemblage. The assemblage, associated with the aggraded condition and bedrock-dominated state, contained almost exclusively coho salmon. The state with a variety of substrate and intermediate amounts of large wood had an assemblage dominated numerically by coho salmon (*O. kisutch*) (85% of the fish present). However, cutthroat trout (*O. clarki clarki*) and steelhead (*O. mykiss*) were also present in relatively large numbers (12.5% and 2.3% of the total numbers, respectively).

The persistence of a population or group of populations (e.g., metapopulation) is dependent on the presence of suitable ecosystem states and the ability of populations to track and use these patches through time. Tracking changes in ecosystem states requires a diversity of suitable connecting habitat. Variation in habitat at small spatial and temporal scales is required for a fish to complete its life cycle and to accommodate a number of life stages or species within a single habitat unit, stream segment, tributary, or watershed. The opportunity for movement across the landscape during various portions of its life cycle (e.g., spawning, over-wintering, ocean migration) is critical for the survival of a local population and opportunities for individuals to move among populations (i.e., stray) are critical for recolonization following local extinctions.

The ability to disperse depends upon distance and habitat conditions along the route of dispersal. Taylor et al. (1993) used the term landscape connectivity to express the degree to which the landscape facilitates or impedes movement among areas. Suitable ecosystem states should exist not only in areas that contain (or could contain) populations, but also across the landscape that provides opportunities for movement as well (Wiens 1997). The term mosaic management (Wiens 1997) has been used to describe efforts to manage movement patterns. This requires that a range of landscape features (i.e., ecosystem states) be considered when determining the fate of local populations in habitat patches.

Changes in type, frequency, and magnitude of natural disturbance can alter abiotic and biotic features and the resilience of an ecosystem (White and Pickett 1985, Hobbs and Huenneke 1992). Resilience of an ecosystem is the capacity of an ecosystem to return to a domain of behavior or range of conditions the system experiences following disturbance (Holling 1973). Changes in the legacy of disturbance may be important in determining the resilience of an ecosystem by altering immediate and future habitat conditions following a disturbance (Reeves et al. 1995). The legacy of a disturbance represents the conditions that exist following a disturbance, and in aquatic ecosystems these conditions are greatly affected by such things as large wood, sediment input and movement, and floodplain function. When the resilience of a system is altered, the domain of behavior may shift and a new system with new, previously unexhibited conditions or states will develop (Reeves et al. 1995, Ebersole et al. 1997). Anthropogenic disturbances, such as timber harvesting and urbanization, may result in disturbances that force systems to a different domain or set of conditions (Yount and Niemi 1990). Gurtz and Wallace (1984) hypothesized that stream biota may not have the capacity to recover from anthropogenic disturbances because they may not have evolved the appropriate breadth of habitat or reproductive requirements, and because such disturbances have no analogues in the natural disturbance regime.

Temporal synchronization of habitat conditions can also result from land-management activities. Historical habitat conditions varied across the landscape creating a shifting mosaic of conditions. Management activities over large areas have resulted in a temporal synchronization of habitat conditions that has resulted in large portions of the range of Pacific salmon and trout to be at a similar state, usually with a reduced capacity for one or more species at the same time (Fig. 1). This situation reduces the range of abiotic conditions and may limit opportunities for the development of various life-history types and for movement of individuals across the landscape. Human activities have altered and constrained the recovery potential of ecosystems,

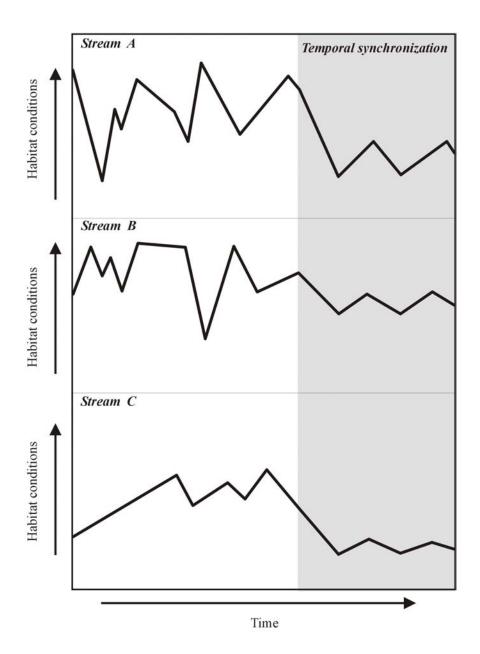


Figure 1. Hypothetical historical conditions followed by temporal synchronization of habitat conditions in three different streams within and among watersheds (Benda 1994, Reeves et al. 1995).

which may be as responsible for the decline of habitat as the direct impact of the original activity (Reeves et al. 1995, Tilman 1996, Ebersole et al. 1997).

When evaluating the extinction risk of Pacific salmon and trout, a static view of habitat conditions may lead to unrealistic expectations of persistence time. The shifting mosaic nature of habitat conditions is discounted if recovery and restoration activities rely solely on a system of reserves. For example, areas set aside for reserves will eventually shift into a less productive state. The loss of reserve habitat cannot be offset by adjacent non-reserve habitat shifting into a productive state if non-reserve habitat is not allowed to recover from human disturbance. Temporal synchronization between reserve and non-reserve areas will result in a continued loss of habitat until the ecological diversity of ecosystems across the landscape can be reestablished. Strategies used in the past for the design and management of reserves focused on species and ecosystems, often ignoring landscape scale and ecological processes relevant at longer time scales and larger spatial scales (Baker 1992). Short-term considerations should include areas with good habitat conditions and functionally intact ecosystems for those areas that remain (Reeves et al. 1995), but long-term considerations must include larger areas. A system made up of disconnected, isolated reserves that are too small to exhibit independent environmental variance (in relation to other reserve areas) increases the risk of metapopulation extinction by reducing opportunities for natural recolonization (Goodman 1987). A reserve system that includes many independent reserves (i.e., exhibit independent environmental variance) across the landscape, and allows for recolonization (i.e., adequate habitat for dispersal among areas) diversity in abiotic and biotic conditions, and adequate time for habitat recovery should provide longer persistence time. Without opportunities for dispersal and recolonization, smaller independent reserves may confer shorter persistence time than a single large reserve (Goodman 1987).

Conclusions

We have identified several critical factors that must be considered if one is to assess the extinction risk of a population or group of populations of Pacific salmon and trout. This is not to dismiss factors such as harvest, influence of hatcheries, and passage mortality. In general, the abiotic and biotic factors to consider are those that provide opportunities for life-history variation to exist, for individuals to move among populations and habitat, and for ecosystems to progress through ecological states over various spatial and temporal scales. We believe that a dynamic ecosystem context is necessary for the extended persistence of Pacific salmon and trout.

As ecological diversity is reduced or lost as a result of a reduction of the abiotic and biotic capacity of the ecological system, opportunities for the expression of phenotypic and genetic variation are reduced or lost. An inappropriate delineation of a population unit may result in an inadvertent misinterpretation of phenotypic characters unique to a particular environment as being nonadaptive, and therefore not incorporating the ecological diversity (i.e., abiotic and biotic) that has allowed that particular population or group of populations to persist. Failed attempts to establish or reestablish populations of Pacific salmon and trout, especially those with more variable life-history types (e.g., sockeye salmon, coastal cutthroat trout), suggest that the local environment is more than a stage to play out a particular phenotype. Wood (1995)

found that reproductively isolated populations of sockeye salmon were adapted to local conditions and were, in some sense, evolutionarily significant. The lack of success in efforts to establish or reestablish Pacific salmon and trout to suitable habitat seems to "fly in the face of the species' apparent phenotypic plasticity and opportunism" (Healey and Prince 1995). Despite many attempts to transplant anadromous sockeye salmon, self-perpetuating anadromous populations have rarely been established, although the establishment of nonanadromous (kokanee) populations from introduction of anadromous populations have occurred (Wood 1995). The failure of anadromous sockeye salmon transplants, despite the establishment of nonanadromous kokanee from these efforts, suggests local adaptation within the donor population for anadromous behavior of sockeye salmon (Wood 1995).

Opportunities for dispersal across the shifting mosaic landscape must be considered when evaluating the extinction risk of Pacific salmon and trout. The extent of structuring of local populations is partially related to the species' life-history patterns and its dispersal capabilities (Avise 1992). Pease et al. (1989) suggested that migration (e.g., dispersal, straying) may often be of greater importance than selection for a population in a changing environment, allowing the population to spatially track a moving environment (i.e., changing environment). Life-history patterns exhibited by a species and opportunities for dispersal are greatly influenced by habitat condition. When populations encounter constraints to tracking environmental change, the population must adapt to local environmental challenges to survive. Even with large population sizes, the extinction risk of a population can increase when opportunities for tracking environmental change (e.g., dispersal) are reduced (Pease et al. 1989). When stray rates are low (or their mortality rate is high), intra-specific variation (local adaptation) may result (Quinn 1997). As dispersal opportunities and suitable habitat are reduced or lost (i.e., greater isolation among populations) due to land use activities, an extinction rate greater than that from the simple loss of habitat area may result (Rieman and McIntyre 1995).

Although the evidence that local adaptation is pervasive and important in populations of Pacific salmon and trout is indirect and circumstantial, observations of local adaptation in other organisms show that it is the result of dynamic processes and it is these processes that must remain intact to preserve genetic diversity (Taylor 1997).

We have attempted to introduce the importance of ecosystem diversity in terms of spatial and temporal variation in abiotic and biotic conditions into the consideration of the extinction risk of Pacific salmon and trout. As Kareiva (1990) pointed out, "simply saying that the spatial environment is important is to mouth a platitude." The examples presented emphasize that variation in abiotic and biotic conditions exists within stream systems and across the landscape of Pacific salmon and trout. This variation is absolutely crucial because it provides the environmental context that these species have evolved in and the context for their recovery and persistence. It is important when assessing the extinction risk of a population of Pacific salmon and trout to recognize the ecosystem processes that generate and maintain the shifting mosaic landscape patterns (Schlosser and Angermeier 1995). Adkison (1995) considers alternatives to the concept of local adaptation. We agree with him that both basic science and conservation efforts would be improved if alternatives are considered, but with fewer and fewer functioning habitats and extent populations, the risk of not assuming local adaptation in the course of land management and conservation decisions may be irreversible.

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